THE TIME OF SEX DETERMINATION IN PLANTS.*

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Having devoted a considerable number of years to cytological investigations, especially on the nature and activity of the chromosomes, and having in the meantime acquired some knowledge of the taxonomy of plants in general and of the nature of their sexual manifestations, the writer at length became aware of the fact that the problems of sex determination, sex differentiation, and sex reversal lie entirely outside of the phenomena of chromosome aggregations and segregations which occur at the fertilization and reduction division periods. Such a conclusion must be evident to anyone who compares a few plant life cycles in relation to these processes or makes a taxonomic study of a series of related plants with bisporangiate, monecious, or diecious flowers. The mere fact that sex determination and segregation usually do not at all coincide with fertilization or reduction in the higher plants and also not in most lower forms, and that such coincidence is confined to a comparatively few out of many types of sexual cycles, made it plain that those botanists who were seeking an explanation of sex determination and sex segregation in a Mendelian formula of homozygous and heterozygous chromosome or factor constitutions were not only following a delusion, but attempting to establish an hypothesis of sexuality that would result in nothing except a contradiction of the most evident phenomena.

A comparison of the various classes of plants from the lowest to the highest and a study of numerous life cycles indicate that practically all plants can be placed into three categories or evolutionary series in respect to their sexual states. The lowest plants are apparent without sex and above these are two groups, each one definitely determined by a transition line, giving two definite evolutionary series. The first transition is from the nonsexual plants to those with sexuality developed only in relation to the gametophyte. If a sporophyte is present

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no sexual states are normally manifest, the universal condition being a homosporous sporophyte individual. The second transition is from plants with sporophytes without sexual states to those with sporophytes showing sexual dimorphism at some stage of their development.

In respect to sex, therefore, all plants can be classified into three general groups. See Chart 1.

I. Plants entirely without sex.

II. Plants in which sexual states and sexual dimorphisms may arise in the gametes or gametophytes, but normally not in the sporophytes if such are present.

III. Plants in which sexual states and sexual dimorphisms arise in the sporophyte, the gametophytes also showing sexual dimorphism and normally always being unisexual.

In both types of sexual plants, so far as they are multicellular, there are numerous independent series of forms ranging from hermaphrodites to unisexual individuals on the one hand and from individuals with bisporangiate sporophylls or flowers to diecious individuals on the other. In both groups the beginning of the establishment of sexual states is near the end of the ontogeny, and in both evolution proceeds by the establishment of the sexual states at earlier and earlier periods in the ontogeny until finally the extreme cases are reached in the sexual state being determined on the one hand during the reduction division, and on the other in the fertilization period. It is self evident, therefore, that some unisexual gametophytes have their sex determined at reduction and others at the beginning of the preceding generation, namely, at fertilization or at some other stage of the sporophyte. Very commonly, and so far as we know perhaps all, unisexual gametophytes which have their sex determined at reduction may have their sexual state reversed to the opposite sex in either direction, and monosporangiate sporophytes which have their sex determined at fertilization may also have their sexual states reversed to the opposite sex in either direction.

In all normal cases sex determination arises but once in the life cycle even though there is an alternation of generations in which it would be possible for the sex to be determined independently for both the gametophyte and sporophyte,

were sex determination dependent on aggregation and segregation of chromosomes.

We can compare the determination of maleness and femaleness with the ordinary process of morphological determination in the ontogeny. In some plants and animals some change is brought about during the process of differentiation which interferes with regeneration so that no reproduction of the individual occurs. In others renewed activity and reproduction of the entire individual are initiated through unusual stimuli.

CHART I.

THE THREE SERIES OR STAGES OF PLANTS IN RELATION TO THE SEXUAL STATE.

Evolution of the sexual state in the sporophyte.	VII. ANGIOSPERMÆ VI. GYMNOSPERMÆ V. PTERIDOPHYTA HETEROSPORÆ	THIRD STAGE. Sexual plants with an alternation of generations, the gametophyte being completely unisexual and the sporophyte always showing some sexual dimorphism, and on all levels except the lowest showing phyletic series ranging from individuals with bisporangiate flowers to monecious and finally dieciou; individuals. Sexuality in the sporophyte attained independently in a number of groups.
Evolution of the sexual state in the gametophyte.	IV. PTERIDOPHYTA HOMOSPORÆ III. BRYOPHYTA II. NEMATOPHYTA	SECOND STAGE. Sexual plants with and without alternation of generations, only the gametes or gametophytes with sexual dimorphism, the sporophyte, when present, normally being in a neutral condition and homosporous, the gametophyte on all levels showing phyletic series from hermaphrodites to completely unisexual individuals. Sexuality attained independently in a number of groups.
Evolution of non-sexual plants.	I. PROTOPHYTA	FIRST STAGE. Plants without sex.

In still others differentiation changes the physiological state of the cell so little that regeneration and somatic reproduction are very general phenomena. Such reproduction often arises in cells highly differentiated morphologically, as when a protonema arises from a liverwort scale or from the diploid, sporophyte tissue of a moss.

Apparently there are similar processes which determine the sexual states in the cell. In some plants the sexual state is easily reversed; in other plants, both gametophytes and sporophytes, reversal is brought about with difficulty or not at all. In the egg or spore then in which sexual states are established, as well as in hermaphrodites, plants with bisporangiate flowers, and monecious plants, sexual states may be strongly or weakly established.

We do not need to be greatly concerned about the more or less equal numbers often maintained between the sexes, which seems to have been the main reason for the Mendelian hypotheses of sex. If we assume that at a certain stage the cell is in a condition of balance or equilibrium so that a slight change of environment, either external or internal, will throw the sexual state in one direction or the other the sex ratio should remain nearly equal. We necessarily are compelled to assume such physiological balances in any event when dealing with certain monecious types where, by a sex determination at a certain point and its reversal at a later stage, more or less constant numerical ratios result of the two types of flowers under a given environment, but which are entirely changed under a new environment. If a constant ratio can be maintained between dimorphic branches on a common axis through changing physiological states, it is not such a very serious challenge when the dimorphism appears in a similarly constant ratio between independent units. The writer has shown that in Arisaema triphyllum, for example, it would be possible to maintain almost any sex ratio desired by a simple environmental control. It is also established that in Cannabis sativa the percentage of sex reversal follows closely the relative length of daylight, so that the actual percentage of reversal for any light period may be predicted about as accurately as the ordinary sex ratios of the higher animals or of the diecious plants.

In those plants in which sexual states arise in the vegetative parts, which is the predominant type, the progression of internal environments, as cell lineage, senility, food supply, relation to more primary tissues, etc., usually are constant enough to put the plant through a regular cycle of sexual expression, just as is the case in the morphological expression, so that it is difficult to change the natural course of events. If, however, we take a plant which has developed an hereditary constitution that unsettles the cell in respect to its sexual states, then the sequence of sexual expression is easily reversed and the part of the flower which should produce stamens may produce carpels or vice versa. This is a common occurrence in such diecious plants as are just across the border line, evolutionally speaking, from the primitive and normal type of bisporangiate angiosperm flowers with the stamens develop first and the carpels above. Familiar examples are various species of Thalictrum, in which in case of reversal stamens or carpels may arise in any position, although the lower bisporangiate Thalictrums have the stamens and carpels in the normal positions, i. e., the stamens below and the carpels above.

In a paper* published by the writer in 1918, entitled "The Expression of Sexual Dimorphism in Heterosporous Sporophytes," the statement was made that: "The sexual state is thrown back, so to speak, into a small part of the sporophyte. It is this spreading of the sexual state, with an ever increasing area of tissue involved, that constitutes one of the most interesting aspects of sporophyte evolution in the higher plants." The evolution of the gametophyte, of course, proceeds in the same way. The difference between a plant with bisporangiate flowers and one with monecious or diecious flowers is a difference in hereditary constitution which induces a male or a female state to be established in the cells or to be reversed at an earlier or later stage of the ontogeny. It is the setting up of a particular physiological condition which activates or controls the expression of hereditary factors into male or female characters that constitutes the real problem to be investigated; and not a search for segregating or associating hereditary factors or "sex chromosomes."

*Ohio Jour. Sci. 18:101-125.

The following diagram (Diagram 1) represents graphically the principal stages of the life cycle of the archegoniates and seed plants at which sex determination or sex reversal takes place in various species. The successive stages show the actual evolutionary progression or phyletic series in relation to the sexual state. It is important to note that whether the gametophyte be hermaphroditic or unisexual, whether the sporophyte be homosporous or heterosporous, there is normally

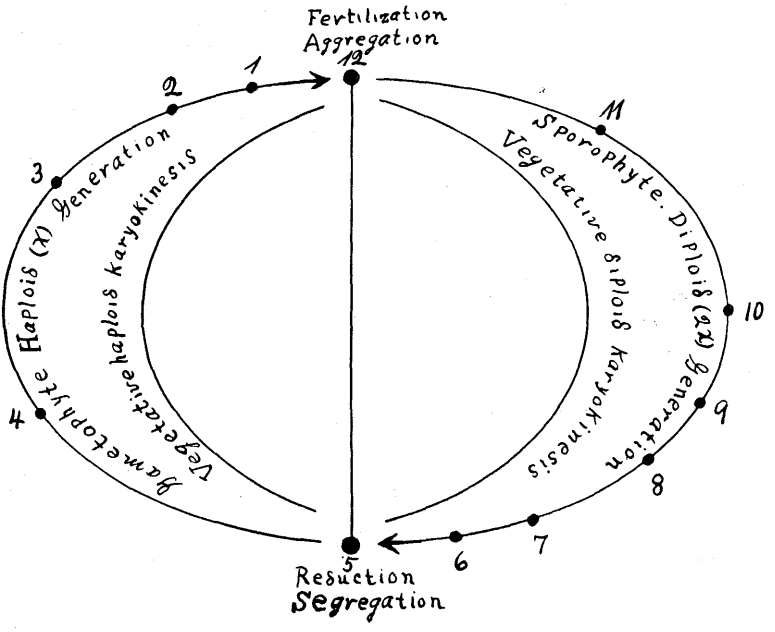

Diagram 1. Showing the various stages at which sex determination takes place in the life cycle in the main types of plants above the thallophytes.

but one stage of sex determination in the life cycle which may, however, be followed soon after by a complete sex reversal. If the sex is determined in the gametophyte there is none in the sporophyte, and if the sex is determined in the sporophyte it remains unchanged through the following gametophyte. The numbers in the diagram represent the following conditions:

1. The point at which sex is determined in plants with hermaphroditic gametophytes and homosporous sporophytes. The sex is determined near the end of the ontogeny of the gametophyte—synoicous, hermaphroditic gametophytes. The

antheridia and archegonia are commingled and sexual dimorphism can appear only in these structures, i. e., between stages 1 and 12.

2. The point at which sex is determined in plants with homosporous sporophytes and paroicous, hermaphroditic gametophytes. In this case sexual dimorphism may be present beyond the gametangia and the opposite sex is expressed farther up on the elongating axis. Sexual dimorphism can appear only between stages 2 and 12.

3. The point at which sex determination takes place in plants with homosporous sporophytes and autoicous, hermaphroditic gametophytes. Entire branches or tips of branches are determined with one sex or the other. Sexual dimorphism is possible between stages 3 and 12.

4. The point at which sex is determined in plants with homosporous sporophytes and with the extreme type of autoicous, hermaphroditic gametophytes in which large branches or branching systems have but one kind of sex organs. In various liverworts and mosses such branches often become separated, giving rise to apparently unisexual gametophytes. Sexual dimorphism may appear between 4 and 12.

5. Time of the reduction division or segregation of chromosomes. If sex determination takes place at this point the gametophytes become unisexual, with possible sex reversal later in the ontogeny of the gametophyte. The sporophyte remains homosporous. Sexual dimorphism is possible in the entire gametophyte, from 5 to 12.

6. The point at which the sexual state is first determined in the sporophyte—heterosporous plants with unisexual gametophytes. Sex determination takes place in the incipient megasporangia and microsporangia or in separate sori on the same leaf or in the floral axis, giving rise to dimorphic sporophylls in the same flower (bisporangiate flowers). Sexual dimorphism present between 6 to 5 to 12.

7. The point at which sex determination takes place in monecious plants with commingled staminate and carpellate flowers, the sex being established at the base of the floral axis. Sexual dimorphism present from 7 to 5 to 12.

8. The time at which sex determination first takes place and is later reversed in monecious plants having inflorescences

with maleness determined below and femaleness above or vice versa. Sexual dimorphism from 8 to 5 to 12.

9. The point at which sex determination takes place, in monecious plants, at the base of the inflorescence, normally without reversal. Sexual dimorphism possible from 9 to 5 to 12.

10. The point at which sex determination takes place in monecious plants having the sporophyte developed with large monosporangiate branches. Sexual dimorphism present to a greater or less degree from 10 to 5 to 12.

11. The point at which sex determination takes place in monecious plants with the main parts of the body differentiated into staminate and carpellate systems. Sexual dimorphism present to a greater or less degree from 11 to 5 to 12.

12. Time of fertilization, or aggregation of chromosomes. The time of sex determination in diecious plants. The sporophytes are entirely monosporangiate under normal conditions, either staminate or carpellate. The determination of the sexual state of the sporophyte and following gametophyte takes place in the egg before fertilization, during the fertilization period or in the early stages of the zygote. Sexual dimorphism is possible in the entire sporophyte individual as well as in the entire gametophyte, i. e., in the entire life cycle from 12 to 5 to 12.

There are, of course, all possible types of intergradation between these main stages. In most cases plants may have determination of sex at an earlier or later stage of development than the normal one. In some species, like Zea mays, there may be much variation, both through the operation of environmental factors and because of differences in hereditary constitution. There is also a possibility of sex reversal in most of the types, except apparently in the gametophytes of heterosporous plants and in a few lower unisexual gametophytes. Specific abnormalities also occur here and there, as for example, cases of apospory and apogamy.

By referring to the diagram it will be seen that at two points in the life cycle the time of sex determination coincides with chromosome shiftings, i. e., in those plants with monosporangiate, heterosporous sporophytes and unisexual gametophytes and in those plants with unisexual gametophytes and homosporous sporophytes. In the former it is possible to apply a homozygous-heterozygous allosome or sex factor formula, in the latter, a

haploid allosome or sex factor formula. The writer has shown by experiments on Cannabis, Humulus, Acnida, Thalictrum, and Arisaema that the homozygous-heterozygous hypothesis is not true, and Mrs. Dorothy Elizabeth Wuist Brown's* experiments with the Ostrich fern show that a segregation, or haploid sex formula, does not hold for unisexual gametophytes having homosporous sporophytes, since she was able to induce sex reversal in both the male and female thalli. The same conditions have been found for the unisexual gametophytes of Equisetum arvense. A glance at the diagram will show that no haploid, segregation allosome, or sex factor can hold for the unisexual gametophytes of heterosporous plants, since the sex is determined before reduction and both cells of the reduction division continue to have the same sex in the gametophyte.

But even if no conclusive experimental evidence were present to show that the hypothesis of Mendelian sex determination is a delusion, would it not be the mark of rashness to assume that the sex determination which takes place at the fertilization and reduction stages must be of a fundamentally different nature, with a new chemistry, physics, or physiology, than the exactly similar sex determination which takes place at the various other stages of the gametophyte and sporophyte ontogenies?

The writer does not at present wish to enter into a discussion of the problem as it affects the higher animals with an allosome difference, except to state positively that the elaborate scheme of sex formulae and nomenclature set up in the past few years has apparently no more foundation on which to rest in the animal kingdom than in the plant kingdom. The whole matter can be consistently explained in an entirely different way. Again, it is necessary to insist on some convincing evidence before the sexuality of plants and of the hermaphroditic animals is divorced from that of the higher unisexual animals.

In the case of an allosome difference it may be true that the difference in heredity between the two bodies may profoundly influence the functional activity of the cell and thus bring about one sexual state or the other, but if this is the case it is in the end only a mode of functional activity of the same nature as when sexual states are determined or reversed in organisms without an allosome difference.

*Wuist, Elizabeth Dorothy. Sex and Development of the Gametophytes of Onoclea struthiopteris, Physiol. Res. 1:93-132. 1913.

As stated above, in both the gametophyte generation of homosporous plants, including bryophytes and homosporous pteridophytes, and in the sporophyte generation of the heterosporous plants, including heterosporous pteridophytes, gymnosperms, and angiosperms, there are numerous repetitions of the evolutionary sequence of sexual states with various intergradations in each series. Thus it is in the gametophyte of the homosporous plants that sexuality is to be studied, since the sporophyte is normally neutral, while in the heterosporous plants, the gametophyte being unisexual, it is the sporophyte that shows the evolutionary progression of the determination of sexual states. In the first, the progression is repeated on practically all levels, the series running from hermaphrodites, often with closely associated organs of the two sexes, through various gradations as synoicous, paroicous, and autoicous, to distinctly unisexual individuals. It must be remembered that all these gradations arise in the presence of the haploid number of chromosomes. In the second, i. e., the hetersoporous sporophyte type, the gradation proceeds from the lowest stage with closely associated microsporangia and megasporangia in the same sorus, to differentiated sori, and then to the more typical bisporangiate flower with distinct microsporophylls and megasporophylls, and from this stage on through the various types of monecious plants to the typical diecious species. These gradations, duplicating those of the gametophyte, appear in the presence of the diploid number of chromosomes.

Below is given a characteristic list of plants, extending from the lower liverworts to the highest dicotyls. This representative list will clearly indicate the relation that exists between the different types of sexual expressions and their independence of aggregating and segregating, Mendelian hereditary units. Such examples could be extended indefinitely, but a study of these given should be sufficient to lead anyone to a comprehension of the real nature of sexuality and the nature of the problems to be solved. Seen in their proper light, they should also be able to clear the minds of any who may have become confused or befogged by the acceptance of the homozygous-heterozygous formula as an explanation of sexuality as it is actually developed in organisms.

Series of species of gametophytes of the homosporous higher plants and of sporophytes of the heterosporous plants to show the nature of the relation of the unisexual state of the individual to the bisexual state.

BRYOPHYTA.

I. Riccia group.—*Riccia crystallina* L., hermaphrodite; *R. michelii* Raddi, unisexual; *Ricciocarpus natans* (L.) Corda, hermaphrodite or apparently sometimes unisexual.

II. Marchantia group.—*Targionia hypophylla* L., hermaphrodite; *Reboulia hemispherica* (L.) Radi, individuals either hermaphrodite or unisexual; *Marchantia polymorpha* L., unisexual but occasionally hermaphroditic individuals have appeared; *Conocephalum conicum* (L.) Dum., unisexual.

III. *Sphaerocarpus terrestris* (Micheli) Sm., unisexual with an allosome difference.

IV. Metzgeria group.—*Metzgeria conjugata* Lindb., hermaphrodite; *M. pubescens* (Schrank) Raddi, unisexual.

V. Fosombronia group.—*Fosombronia foveolata* Lind., hermaphrodite (either synoicous or paroicous); *F. wondraczeki* (Corda) Dum., hermaphrodite (paroicous); *F. caespitiformis* De Not., hermaphrodite (paroicous) and unisexual; *F. angulosa* (Dicks.) Raddi, unisexual.

VI. Cephalozia group.—*Cephalozia bicuspidata* (L.) Dum., hermaphrodite (autoicous); *C. lammersiana* (Hueb.) Spruce, hermaphrodite (autoicous) or apparently unisexual by the separation of male and female branches; *C. serriflora* Lind. unisexual.

VII. Cephaloziella group.—*Cephaloziella elegans* (Heeg) K. M., hermaphrodite (paroicous); *C. striatula* (Jens.) Douin, hermaphrodite (autoicous but occasionally paroicous); *C. hampeana* (Nees) Schiffn., hermaphrodite (autoicous); *C. myriantha* (Lind.) Schiffn., hermaphrodite (paroicous) and occasionally pure male and female individuals produced; *C. starkei* (Funck) Schiffn., unisexual.

VIII. Frullania group.—*Frullania saxicola* Aust., hermaphrodite (autoicous); *F. tamarisci* (L.) Dum., this and most species of the genus unisexual.

IX. Bog-moss group.—*Sphagnum rigidum* Schp., hermaphrodite; *S. squarrosum* (Pers.) Schwaeg., either hermaphrodite or unisexual; *S. cymbifolium* Ehrh., unisexual.

X. Granite Moss group.—*Andreaea petrophila* Ehrh., hermaphrodite (autoicous); *A. nivalis* Hook., unisexual.

XI. Grimmia group.—*Grimmia apocarpa* (L.) Hedw., hermaphrodite (autoicous); *G. alpestris* Schleich., unisexual or rarely hermaphroditic (autoicous); *G. trichophylla* Grev., unisexual.

XII. Bryum group.—*Bryum arcticum* R. Br., hermaphrodite (synoicous); *B. provinciale* Philib., hermaphrodite, often synoicous and autoicous branches on the same plant; *B. warneum* Bland, hermaphrodite

(autoicous, rarely synoicous); *B. marratti* Wils., hermaphrodite (autoicus); *B. roseum* Schreb., unisexual.

XIII. Hypuum group.—*Hypuum polygamum* Schp., hermaphrodite (synoicous or autoicous); *H. riparium* L. hermaphrodite (autoicous); *H. exannulatum* Guemb., unisexual, rarely hermaphroditic (autoicous); *H. aduncum* Hedw., unisexual.

XIV. Splachnum group.—*Splachnum ampullaceum* L., hermaphrodite (autoicous); *S. vasculosum* L., unisexual.

XV. Hair-cap Moss group.—*Catharinaea undulata* Web. & Mohr., hermaphrodite (synoicous and paroicous); *C. tenella* Roehl., unisexual; *Polytrichum commune* L., unisexual. The tendency in the higher mosses is to be unisexual.

Pteridophyta Homosporæ.

XVI. Eusporangiate ferns.—*Botrychium virginianum* (L.) Sw., hermaphrodite; *Marattia douglasii* (Presl) Baker, usually hermaphroditic, but sometimes thalli appear with only antheridia present.

XVII. Leptosporangiate ferns.—*Adiantum capillus-veneris* L., hermaphrodite; antheridia develop first and later toward the anterior end an area of archegonia is developed; *Pteretis nodulosa* (Mx.) Nieuwl., American Ostrich-fern. (*Onoclea struthiopteris* L. of authors), typically unisexual. According to the investigations of Mrs. Elizabeth Dorothy Wuist Brown, about 15% of the thalli in old cultures in soil were hermaphroditic. She was able to induce 90% of the female thalli later to produce antheridia. Only 5% of the male thalli were induced later to produce archegonia.

XVIII. Equisetum.—*Equisetum laevigatum* A. Br., thalli hermaphroditic, *E. arvense* L., thalli unisexual with sex reversal in both directions, but more commonly the females changing to the male condition. Note: So far as known, in both the leptosporangiate ferns and in the horsetails, the unisexual thalli occur in the species with the most highly evolved sporophytes.

XIX. Lycopods.—*Lycopodium complanatum* L., has hermaphroditic gametophytes.

Heterosporous Sporophyte Series, the Gametophytes Being Unisexual.

XX. Heterosporous Pteridophytes.—*Marsilea quadrifolia* L., microsporangia and megasporangia in the same sorus; *Salvinia natans* (L.) Hoff., microsporangia and megasporangia in distinct sori on the same leaf; *Selaginella rupestris* (L.) Spring., microsporangia and megasporangia on distinct sporophylls, but on the same floral axis; i. e., flowers bisporangiate.

Angiospermæ.

XXI. The Lowest Helobiæ.—*Echinodorus cordifolius* (L.) Griseb., flowers bisporangiate; *Lophotocarpus calycinus* (Engelm.) Sm., bispor-

angiate in lower part of inflorescence, staminate with vestigial carpels in the upper part; *Sagittaria longirostris* (Micheli) Sm., monecious, with carpellate flowers below and staminate above or sometimes the entire inflorescence staminate or carpellate; doubtful whether there are really diecious individuals; *Burnatia enneandra* (Hochst.) Micheli, diecious.

XXII. Palms.—*Sabal palmetto* (Walt.) R. & S., flowers bisporangiate; *Cocos nucifera* L., monecious, the staminate and carpellate flowers on the same inflorescence with occasional intermediate flowers on the transition tissue; *Phoenix dactylifera* L., diecious, but occasionally with sex reversal at least on the staminate plant. Note: Palms of all gradations of sexual expression occur between the bisporangiate and diecious types.

XXIII. Aroids.—*Acorus calamus* L., flowers bisporangiate; *Peltandra virginica* (L.) Kunth., monecious, with a transition zone between the carpellate flowers below and the staminate above; *Ariseama dracontium* (L.) Schott., monecious and staminate individuals, the staminate usually greatly predominating; monecious individuals ranging from those having only a few carpellate flowers below to those with only a few staminate flowers above; sex reversal of both types general, the staminate to monecious, and the monecious to staminate; *Arisaema triphyllum* (L.) Torr., diecious, with a considerable percentage of monecious individuals ranging from almost completely staminate; to almost completely carpellate sex reversal in all types of individuals general in all directions.

XXIV. Sedges.—*Scirpus validus* Vahl., flowers bisporangiate; *Cymophyllus fraseri* (Andr.) Mackenz., monecious, the spikelet carpellate below and staminate above; *Carex gracillima* Schwein., monecious, spikelets staminate below, carpellate above; *C. lupulina* Muhl., monecious, the entire spikelets are either carpellate or staminate; *C. exilis* Dewey, sometimes diecious, sometimes with staminate flowers above and carpellate flowers below, and sometimes with carpellate flowers above and staminate below; *C. dioica* L., diecious.

XXV. Grasses.—*Festuca elatior* L., flowers bisporangiate; *Panicum virgatum* L. Spikelets with a bisporangiate and a staminate flower; *Andropogon furcatus* Muhl., with paired spikelets, one with a bisporangiate flower, the other with a staminate flower; *Zizaniopsis miliacea* (Mx.) D. & A., monecious, the panicle with carpellate spikelets and staminate spikelets, the carpellate borne at the base of the branches and the staminate at the ends; *Zizania aquatica* L., monecious, staminate spikelets in the lower part of the panicle, and carpellate spikelets at the upper end, with spikelets containing bisporangiate flowers on the transition zone; *Tripsacum dactyloides* L., monecious, the lower part of the inflorescence with carpellate spikelets and the upper with staminate spikelets; *Zea mays* L., monecious, normally with completely distinct staminate and carpellate inflorescences, but often with many intermediate developments; *Scleropogon karwinskyanus* (Fourn.) Benth., diecious; *Bulbilis dactyloides* (Nutt.) Raf., diecious, but apparently monecious individuals have been reported.

XXVI. Bunch-flower sub-family.—*Anticlea elegans* (Pursh) Rydb., flowers bisporangiate; *Zygadenus glaberrimus* Mx., flowers mostly bisporangiate; *Stenanthium robustum* Wats., inflorescence with bisporangiate and monosporangiate flowers; *Melanthium latifolium* Desr., monecious, both sorts of flowers scattered in the same inflorescence, probably with some intermediate flowers; *Chamaelirium luteum* (L.) Gr., diecious.

XXVII. Thalictrum group.—*Thalictrum clavatum* DC., flowers bisporangiate; *T. dasycarpum* Fisch. & Lall., flowers bisporangiate or monosporangiate, plants monecious to diecious with change of sexual expression in the individual from time to time; *T. revolutum* DC., diecious or some plants with both stamens and carpels; *T. dioicum* L., diecious, with occasional individuals of various grades of intermediateness.

XXVIII. Clematis group of genera.—*Atragene americana* Sims, flowers bisporangiate; *Clematis virginiana* L., diecious with some intermediate flowers occasionally present.

XXIX. Spurge group.—*Geranium maculatum* L., flowers bisporangiate; *Callitriche austeni* Engelm., with bisporangiate and monosporangiate flowers; *Croton monanthogynus* Mx., monecious with commingled flowers; *Ricinus communis* L., monecious with staminate flowers on the lower part of the panicle and carpellate flowers above; occasionally with bisporangiate flowers on the transition zone; *Stillingia sylvatica* L., monecious, with carpellate flowers below and staminate above; *Chamaesyce maculata* (L.) Small, monecious, with reduced carpellate and staminate flowers close together in a cyathium; *Mercurialis annua* L., diecious with some intermediate individuals; *Croton texensis* (Klotzsch) Muell., diecious, with considerable vegetative sexual dimorphism.

XXX. Amaranth group.—*Froelichia campestris* Small, flowers bisporangiate; *Amaranthus spinosus* L., monecious; *Amaranthus palmeri* Wats., diecious, with intermediates; *Acnida tamariscina* (Nutt.) Wood; diecious, with occasional sex reversal in both staminate and carpellate plants.

XXXI. Rumex group.—*Oxyria digyna* (L.) Hill, flowers bisporangiate; *Rumex crispus* L., with bisporangiate and carpellate flowers on the same plant; *Rumex altissimus* Wood., monecious with vestiges in both the staminate and carpellate flowers; *Rumex acetosella* L., diecious.

XXXII. Rose family.—*Duchesnea indica* (Andr.) Focke, flowers bisporangiate; *Poterium sanguisorba* L., with bisporangiate and monosporangiate flowers in the heads; *Fragaria vesca* L., diecious, with monecious individuals; *Aruncus aruncus* (L.) Karst., diecious.

XXXIII. Bean family.—*Hoffmanseggia jamesii* T. & G., flowers bisporangiate; *Gleditsia triacanthos* L., with bisporangiate and monosporangiate flowers; *Gymnocladus dioica* (L.) Koch, diecious, both flowers with prominent vestiges.

XXXIV. Maple group.—*Staphylea trifolia* L., flowers bisporangiate; *Aesculus glabra* Willd., monecious, both flowers in the same

cluster; *Acer platanoides* L., diecious, with frequent reversals of flowers or branches to the opposite sex; *A. saccharinum* L., diecious, with sex reversal in both directions; *A. negundo* L., diecious.

XXXV. Nettle group.—*Ulmus americana* L., flowers bisporangiate; *Parietaria pennsylvanica* Muhl., with bisporangiate and monosporangiate flowers; *Humulus japonicus* Sieb. & Zucc., diecious, with sex reversal in either direction; *Cannabis sativa* L., diecious, with no vestiges in the flowers but with distinct vegetative dimorphism, some races with monecious individuals, mostly with abundant sex reversal in either direction under proper environment, especially under short light periods alternating with long periods of darkness.

XXXVI. Woody amentifers.—*Alnus incana* (L.) Willd., monecious; *Myrica gale* L., diecious, with sex intermediates and with sex reversal in either direction; *Salix amygdaloides* Anders., diecious with occasional monecious individuals; *Populus deltoides* Marsh., diecious.

XXXVII. Evening primrose type.—*Oenothera biennis* L., flowers bisporangiate; *Proserpinaca palustris* L., flowers bisporangiate; *Myriophyllum heterophyllum* Mx., monecious, with carpellate flowers below and staminate above on the inflorescence and with bisporangiate flowers on the transition zone; *Myriophyllum proserpinacoides* Gill., is said to be nearly diecious; *Fuchsia procumbens* Cunn., diecious.

XXXVIII. Cucurbit group.—*Asarum canadense* L., flowers bisporangiate; *Cucumis melo* L., monecious, but often with some functional bisporangiate flowers; *Cucurbita foetidissima* H. B. K., monecious; *Sicyos angulatus* L., monecious, staminate and carpellate inflorescence arising from the same node; *Bryonia alba* L., monecious; *Bryonia dioica* L., diecious.

XXXIX. Ebony group.—*Bumelia lycioides* (L.) Pers., flowers bisporangiate; *Symplocos tinctoria* (L.) L'Her., with bisporangiate and staminate flowers; *Diospyros virginiana* L., diecious.

XL. Fraxinus group.—*Syringa vulgaris* L., flowers bisporangiate; *Fraxinus ornus* L., flowers bisporangiate or imperfectly bisporangiate; *F. quadrangulata* Mx., flowers bisporangiate or imperfectly bisporangiate; *F. americana* L., diecious.

XLI. Plantain group.—*Plantago rugelii* Decne., flowers bisporangiate; *Littorella uniflora* (L.) Asch., monecious, with decided dimorphism of the peduncle; *Plantago heterophylla* Nutt., diecious, with some bisporangiate flowers; *P. virginica* L., diecious.

XLII. Valeriana.—*Valeriana pubicarpa* Rydb., flowers bisporangiate; *V. edulis* Nutt., imperfectly diecious, with bisporangiate and monosporangiate flowers; *V. acutiloba* Rydb., diecious and dimorphic.

XLIII. Ragweed group.—*Iva ciliata* Willd., monecious, marginal flowers of the heads carpellate, central flowers staminate; *Ambrosia trifida* L., monecious, carpellate heads below, staminate heads above.

XLIV. Composits.—*Lacinaria scariosa* (L.) Hill, flowers bisporangiate; *Inula helenium* L., outer, ray flowers carpellate, inner, disk

flowers bisporangiate; *Silphium perfoliatum* L., monecious, outer flowers carpellate and inner staminate; *Baccharis salicina* T. & G., diecious; *Antennaria plantaginifolia* (L.) Rich., diecious, with dimorphic inflorescence.

XLV. Genus Artemisia.—*Artemisia tridentata* Nutt., all the flowers bisporangiate; *A. absinthium* L., marginal flowers carpellate, central flowers bisporangiate; *A. caudata* Mx., marginal flowers carpellate, central flowers staminate.

XLVI. Genus Cirsium.—*Cirsium undulatum* (Nutt.) Spreng., flowers bisporangiate; *C. arvense* (L.) Scop., diecious or imperfectly diecious.

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